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INFLUENCE OF HIGHER PLANTS UPON EACH OTHER—ALLELOPATHY

Some new results of research into allelopathy

BY

ANTS AAMISEPP and HUGO OSVALD

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ANTS AAMISEPP and HUGO OSVALD[1]

Introduction

In studying natural plant communities and crops of different kinds it soon becomes evident that higher plants. trees and shrubs, herbs and grasses, exercise a considerable influence upon each other. Certain species. in natural plant communities as well as on cultivated land and meadows, thrive very well together, other less well. some crops are weed attracting, others keep the weeds away. To an important extent this influence can be explained by differences in the plants' ability to compete for space and light, for water and nutrients or, in other words, for abiotic growth factors. Some species become predominant over others because of rapid growth, through their morphology, by leaf shedding or by means of a well-developed root system, others may take advantage of tolerance to unfavourable growth conditions, such as low temperatures, long lasting drought periods or through modesty of demands upon nutrients in the substrate.

Many of the phenomena that can be observed in the communal growth of plants cannot, however, be explained merely as a consequence of competition involving abiotic growth factors. On the contrary, one is forced to suppose that the higher plants also have other weapons in the struggle for existence, for instance different kinds of physiologically active substances—exuded from roots or other parts of the plants—with stronger or weaker biological effects upon other plants. Many observations from Swedish crop production sustain the supposition that root exudates from certain plants exercise a biotic effect, stimulating or retarding, on other species, and sometimes also on other individuals of the same species, in their immediate neighbourhood.

In studying this big and complicated problem the role played by microorganisms in the ultimate outcome of the competition between the higher plants cannot be neglected.

It is fairly well known that many lower organisms exude substances with evident effects upon other lower organisms. A well-known substance of this kind is penicillin, which is exuded by fungi of the genus *Penicillium*, and which has a pronounced retarding effect upon the growth of many bacteria. Several substances with similar effect have recently been isolated and produced in pure form and have been widely employed under the name of antibiotics. Other lower organisms exude substances with a favourable influence upon other organisms, as is the case for instance with the nitrogen-fixing and nitrite- or nitrate-exuding bacteria, such as *Azotobacter*, and blue-green algae, such as *Tolypothrix*.

Retrospective review

Although our knowledge concerning physiologically active exudates from higher plants is still limited, the result of this phenomenon has been observed for a long time. As far as we know, the oldest statement, indicating that its author was aware of or at least surmised that a peculiar kind of influence occurred, dates from the first half of the eighteenth century. It is a Swedish author who advises farmers upon the control of wild oats, *Avena fatua* L., or land oats as it was called at that time. He writes: "If you have a lot of land oats in your fields, you should plant rye, because it kills the land oats."[2] In a reply to a prize-problem, formulated by the Royal Academy of Science,

[1] Our cordial thanks are due to Professor Harry Godwin, F.R.S., Cambridge, for his kindness in revising the translation into English of this paper.

[2] "Om du har fått mycket landhafra i din åker, då skall du så råg, ty han dräper landhafran."

on how most effectively to control wild oats, SIÖSTEEN (1749) recommends planting of rye as the most reliable method, and two years later JOHAN BRAUNER (1751) writes: "It is hard to be troubled with land oats. Certainly, among the rye it does not thrive; but when barley is planted on the rye field, it will again flourish thanks to the seeds that have been spread along the edges of the ditches and the road sides."[1]

It is not clear from the eighteenth century literature, how the remarkable influence of the rye was regarded. It is, however, of interest to establish that these observations have been made. It is a matter of observation that wild oats are very rarely found in a rye field.

In recent times the problem of the ability of higher plants to exude active substances has frequently been discussed in relation to problems concerning the plants' struggle for space and with soil infertility.

The idea that certain plants excrete poisonous substances is in reality not a new one. Already in 1832 DE CANDOLLE advanced his toxin theory, which implies that the grouping of plants in natural plant communities is due to the fact that certain plants secrete from their roots substances detrimental to others. The secretions were conceived as waste products of the plants' metabolism. From his toxin theory DE CANDOLLE also deduced his crop rotation theory. Among the earliest supporters of the toxin theory was also LIEBIG.

Unfortunately however, the toxin theory had an insufficient experimental foundation, and when shortly afterwards LIEBIG's so-called "mineral theory" made a victorious progress all over the world, the toxin theory was more or less forgotten. Certainly, in the nineteenth century a few scientists expressed their sympathy for DE CANDOLLE's theory (see for instance LIVINGSTON 1907), but they were unable to answer the objections against it. Not until the beginning of the twentieth century did scientists at the U.S. Bureau of Soils (WHITNEY and CAMERON 1904; LIVINGSTON, BRITTON and REID 1905; LIVINGSTON 1907; SCHREINER and REID 1907; SCHREINER and SHOREY 1909; *inter alia*) seriously get to work upon the subject. In studying the causes for varying fertility of a number of soils these investigators had arrived at the conception that the differences could only be explained by the supposition that certain soils contained toxic organic substances that prevented a normal development of particular cultivated plants. Clover and wheat grown on such soils became stunted. The symptoms were described for instance as follows (LIVINGSTON, BRITTON and REID 1905): "The stems and leaves are short; the former are slender and the latter narrow. The primary roots fail to develop to normal length and exhibit an increase in diameter, often having swollen regions, especially at the tips. Root branches are almost entirely absent even at the end of three weeks' growth, and the few existing ones are extremely short."

The work at the Bureau of Soils permitted the conclusion that from an infertile soil two organic substances had been isolated, one containing nitrogen (picolinic acid) and one nitrogen-free, (dihydroxystearinic acid), both decidedly toxic to plants, even at a concentration of 1:10,000, and which "like many poisons had a stimulating effect when present in small quantities" (SCHREINER and SHOREY 1909, p. 52).

It would lead too far here to review the plentiful literature on this so-called toxin theory, for which the director of the Bureau of Soils, WHITNEY, became the foremost spokesman. However, at this time also the theory met with strong opposition, and since it had not in any case been possible to prove that the substances mentioned were secretions from roots, the toxin theory was again rejected in spite of the great amount of experimental evidence of the kind mentioned above that its supporters were able to present.

When one of us, OSVALD, in 1915–1924 was engaged in ley experiments at the Experimental Farm Flahult of the Swedish Peat Reclamation Society and at a number of farms in Middle Sweden, where the Agricultural Society of Sweden (now the Agricultural Union) carried out its agricultural experiments, on several occasions observations were made, that could be explained as due to some peculiar physiologic competitive ability of certain grass species. For instance, pure stands of some species were nearly free from weeds, while pure stands of other species were heavily infested with weeds. In a report on these experiments the following statement was made concerning the tall oat grass, *Arrhenatherum elatius* M. & K. and red fescue, *Festuca rubra* L.: "Consequently, the

[1] "Landhafran är svår att dragas med. Det är wist, at ibland rågen har hon ingen trefnad; men när korn kommer at sås på råglandet, så får hon åter fri luft genom de fröen, som sått sig wid renarna."

tall oat grass not only has the ability to thrive in pure stands, but due to the uniformity of the stand and *a probably well equipped root system*[1] it seems to be able to keep the weeds away much better than other grasses.—The very dense carpet of red fescue also remains pure" (OSVALD 1926, p. 104). Concerning the tall oat grass the following statement was also made: "This grass has a peculiar ability to eradicate clover." Since the tall oat grass never can cover the soil surface in the same way as the carpet-forming grasses such as red fescue, but nevertheless is able to keep other species away, some other factor must be involved. Consequently, it is conceivable that also in the case of red fescue the deciding factor is some factor other than the density of the plant carpet. However, at that time there was no opportunity to start research on this problem.

It may be mentioned here, that in the 1920's experiments were carried out at the Agricultural Experiment Station at Kingston, R.I., U.S.A., on the effect of cultivated plants upon each other. During a visit to Kingston in 1927 one of us, OSVALD, had an opportunity to study these experiments. The director of the station, BURT L. HARTWELL, had begun a great investigation to identify the influences of different cultivated plants upon succeeding crops. In this respect great differences had been found. HARTWELL explained his results as follows: Plants with alkaline ash, i.e. those that take up relatively much bases from the soil, leave the soil in a more acid condition than do plants with a more acid ash. In the more acid soil, HARTWELL assumed, the toxic aluminium ion is activated and that might explain the differences between different species with regard to their value as preceding crops (HARTWELL, SMITH and DAMON 1927). However, it has later been proved (*inter alia* by MATTSON and HESTER, 1933), that the aluminium ion does not become activated except at relatively low pH-values, which may not have occurred in the soils, where HARTWELL carried out his experiments. It is then not unreasonable to assume that the differences in after-effect may be due to secretions from the roots or from decomposition products of the organic material.

With the discovery of plant hormones in the late nineteen-twenties (WENT 1928) it was realized that certain organic substances produced by the plants themselves, in extremely small concentration stimulate or retard the growth of plants. It was also found that some species were very susceptible, others less susceptible to these substances. Through these discoveries research concerning the influence of higher plants upon each other (i.e. the toxin theory) attracted renewed interest. This interest was further stimulated by the discovery of penicillin and the intense research on antibiotics that followed it. Moreover, in recent years it has been found that higher plants as well as the lower contain antibiotic substances. It has been shown that the role played by several medical plants in the popular medical art of old days is due to their content of bacterium-killing substances (*Monthly Science News*, no. 7, 1945). Antibiotic substances may be secreted from roots or from other organs but in recent years the attention of ecologists has mainly been directed to the root exudates.

In the middle of the 1940's, through the advent of the so called hormone derivatives, weed control research was turned on to new tracks and at the Department of Plant Husbandry of the Royal School of Agriculture observations on the relationships between weeds and cultivated plants were actively initiated and directed to the problem of the effects of root exudates. However, it was impossible to begin with to devote much time to this problem, as several other urgent problems had priority. Some small experiments were, however, carried out. For instance, in a small pot experiment it was demonstrated, that rye had a rather inconsiderable effect on the germination of wild oats but strongly retarded the development of the young plants, an observation according with the old dictum "he kills the land oats". An observation made in the autumn of 1945 on the effect of couch-grass (*Agropyrum repens* P.B.) on rape gave rise to a series of experiments in which the effect of extracts of roots and rhizomes of couch-grass upon the germination of rape and oats and the subsequent development of the seedlings of these species was studied (see below) (OSVALD 1947).

In a subsequent experiment the effect of soil extracts on the germination of rape was studied. Two soils were employed, one from a grass ley with a very dense carpet of red fescue, one from a cultivated field at Kungsängen at Uppsala. It turned out that the extract from the red-fescue soil strongly retarded the germination of rape. In this case there could hardly be

[1] Italicized here.

any doubt but that the effect was due to a root exudate. In another series of experiments a number of grasses were grown on filter paper. The grasses with their roots were then removed and the filter paper was used for germination experiments with rape. The result was that although the effect on the germination was slight, the effect of the root exudates of some of the grass species on the development of the seedlings was quite considerable (OSVALD 1949).

During the continued, rather comprehensive weed control experiments at the Department of Plant Husbandry, observations were made, which encouraged us to make more detailed studies of the influence of different species upon one another. One of these for instance was that scentless mayweed, *Matricaria inodora* L., and rape seemed to thrive very well together. But once again other, more urgent tasks had to be given preference. Not until 1958, when a research grant had been received from King Gustaf VI Adolf's Foundation for Swedish Culture, was it possible to begin a comprehensive series of experiments. His Majesty the King of Sweden had already as Crown Prince during a visit to the Royal School of Agriculture seen some experiments on the effect of couch-grass on rape and had become highly interested in the problem.

The experiments have been planned in detail by both of us, and then ANTS AAMISEPP and PAUL RACZ took charge of the experimental work and the elaboration of the results. After the tragic, sudden decease of Paul Racz, Aamisepp has continued the work and elaborated the results.

It should be added that after the experiments carried out with the support from the Royal Foundation in 1958 and 1959 had been concluded the research was enabled to continue by means of research grants from the Ekhaga Foundation.

It is a pleasing task on this occasion to convey our warmest thanks for the grants which have made it possible for us to carry out the work now presented.

Review of literature

Before proceeding to an account of our research on allelopathy at the Department of Plant Husbandry it is appropriate to give a short review of the abundant literature on the problem published in recent years. In doing so, we have had to confine ourselves to those publications recording the isolation and identification of active substances and investigation of their physiological effects.

Ever since 1937, when MOLISCH's work on the influence of plants upon each other, which he designated as allelopathy, was published, the study of the mutual influence of plants has in many quarters been studied with great interest and in many places. MOLISCH, like many previous scientists, had not dealt separately with the lower and higher plants. GRÜMMER (1955) was the first who confined the term allelopathy to the effect of higher plants upon each other.

The active substance may be a gaseous excretion, a liquid or a solid substance, and it may either be secreted from living plant organs, such as roots, leaves, fruits and seeds, or be formed by the decomposition of dead plant tissues.

To begin with we shall here discuss secretions from plant organs in the soil and then from plant organs above the soil. The secretions from the roots, so called root exudates, have attracted much interest from the point of view of plant crop production.

The question whether the organic substances are actively secreted from living, functioning root cells or are liberated from dying cells of perpetually decomposing cortex, calyptra or root hairs has been obscure for a long time. Only recently two German scientists (EBERHARDT and MARTIN 1957; MARTIN 1957) have been able to show, directly under the fluorescence microscope, the secretion of scopoletin (7-hydroxy-6-methoxy-coumarin) from cells of oats roots grown in distilled water. This seems to be the only instance in which secretions from living cells have been demonstrated. Further, they found that the secretion was considerably greater under unfavourable growth conditions than under optimal ones. It has not been possible to demonstrate the occurrence of scopoletin in free form in the soil, which indicates that it is rapidly decomposed by microorganisms. Consequently, this particular active root secretion seems to be of minor importance in nature in the mutual influence of higher plants.

The substance liberated from dying root cells seems to have a greater allelopathic importance, but its effect can not be kept apart from that of real secretions. A rather interesting instance of root secretions is given by BONNER and GALSTON (1944) in an account of work with the guayule shrub, *Parthenium argenta-*

tum A. Gray, a shrub from Central America, which is cultivated in North and Central America for the extraction of rubber. From the roots of old guayule plants the two scientists were able to isolate a substance that was identified as trans-cinnamic acid. This substance had a strongly retarding effect on the growth of seedlings of the species. In the soil the trans-cinnamic acid is rapidly broken down by micro-organisms, and its effect on other higher plants is probably insignificant.

It has also been found that many other species, among them oats, wheat, maize, peas, potatoes and several species of ley grasses, clover and lucerne secrete substances from their roots. The most important of the active substances that have been isolated and identified are amino acids, sugars, flavones, nucleotides and unsaturated lactones.

Secretions from leaves seem to play a greater role in nature in the plants' struggle for space. Gaseous secretions of essential oils occur in a great number of medicinal and aromatic plants. They are mostly secreted from leaves or flowers and they are usually poisonous both to higher plants and to micro-organisms. The secretion from the classical "burning bush of Moses", the diptam shrub, *Dictamnus alba* L., is so strong that the air surrounding the shrub in calm weather can be set on fire.

The volatile oils, however, rarely occur in concentrations high enough to endow them with any appreciable ecological importance in nature.

Concerning other secretions from leaves it can be stated that most of them are washed out by rain and that in the soil they may then affect other plants. In most cases they are nutrients leached out from the leaves but in some cases it has been shown that they are physiologically active in other ways. For instance Bode (1940) has found that a strongly growth-retarding substance is leached out by rain water from the leaves of the wormwood, *Artemisia absinthium* L. This substance, which has been identified as absinthin, strikingly inhibited the growth of *Foeniculum vulgare* Mill. and certain other species.

Another very good example of active substances leached from leaves is provided by *Encelia farinosa* A. Gray, a shrub growing in the desert region of southern California. Long ago it had been observed that the herbage below this shrub was rather sparse and poor in species, in spite of the seemingly weak competitive power of the plant in comparison with other shrubs. Gray and Bonner (1948*a*, 1948*b*) proved that it was the leaves that contained the active substance, and that it had a strongly growth-retarding effect on certain herbs but did not affect plants of the same species. With rain drops and through leaf fall this substance is brought into the soil, where it has a long-lasting effect, since it is not leached out in the dry climatic conditions prevailing in the desert. The active substance was isolated by the two scientists concerned and was later identified as 3-acetyl-6-methoxybenzaldehyde.

Among secretions from leaves the strongly retarding substances of the leaves of the walnut tree, *Juglans nigra* L., may be mentioned. They are washed into the ground by rain-water, where they may affect other species, such as potatoes and tomatoes among others. As one of the substances secreted Bode (1940) was able to identify the toxic principle juglone. The others were supposed to be tannins.

Finally it should be emphasized that Grümmer (1959) has found that rain drops from the leaves of false flax, *Camelina linicola* Sch. & Sp., a bad weed in flax fields, leach out a substance, which has a strongly retarding effect upon flax. So far it has not been possible to identify this substance.

It has long been a well-known fact that fruits and seeds secrete physiologically active substances. The occurrence of substances inhibiting germination is a common phenomenon and has been shown in more than a hundred species. Their effect is not specific. The classical example is Molisch's (1937) detailed studies on the effect of ethylene on different plants and plant organs. Already at the turn of the century it had been observed that coal-gas damaged trees, and that if a bunch of ripe bananas was placed in a box together with green, unripe bananas, the ripening of the latter was accelerated. Through Molisch's work it was made probable that in this case ethylene was the active substance. He also showed that ripe apples secreted ethylene that had a growth retarding effect on the roots and stems of seedlings. It has, however, not been proved that ethylene was the active substance in Molisch's experiments. The fact is that several scientists have later been able to show that "apple air" contains at least 20 different gaseous components.

Further, in rather simple experiments it has been possible to show that germinating beet seeds liberate

ammonia, which prevents the germination of seed of corn cockle, *Agrostemma githago* L., but also in this case the physiological effect may be due to other substances.

The presence of germination-inhibiting amino acids and sugars has been shown in swollen grains of rye, wheat and barley and seeds of ley grasses and clover. Among other retarding or inhibiting substances the following may be mentioned: flavones (quercitin, myricetin *inter alia*) unsaturated lactones and phenols: these are secreted from swollen seeds of clover, lucerne, sweet clover (melilot), and flax (linseed).

However, so far in no case has it been possible to show that germination inhibiting substances are present in a free state in the soil.

In agricultural research much more attention has been directed towards toxic substances liberated in the soil when plants are decomposed, and the consequent so-called soil sickness. The oldest conception of this infertility phenomenon seems to be that the toxins, which were formed during the decomposition of plant debris, made the soil poisonous, but the role of plant debris in this connection has been and still is the object of much interest.

Several scientists, among them COLLISON (1925) and BÖRNER (1956), have been able to show that water extracts from rye, wheat, barley, and oats as well as soil extracts from stubblefields of these crops contain toxic phenolic compounds. In some instances these substances have been isolated and identified. Some such substances, identified by means of paper chromatography are ferulic acid, vanillic acid, *p*-coumaric acid, and *p*-hydroxybenzoic acid. These substances, produced synthetically, have been found to have the same effect as those isolated from the plants.

In order to illustrate the problem of soil infertility some recent investigations may be briefly reviewed. A group of German scientists, BÖRNER, MARTIN, CLAUSS, and RADEMACHER (1959), studied soil infertility with regard to flax as compared to that for rye. These plants were grown in nutrient solutions in which the nutrient level was kept constant. It was found that flax grown following flax had 12 per cent shorter stems and 33 per cent lower dry weight than flax grown for the first time in the same solution. The corresponding figures for rye were 1 and 15. After detailed investigations in order to clear up the causes for this result, these scientists arrived at the conclusion that allelopathic factors must play a role in soil infertility for flax in addition to the effect of parasites.

Soil sickness has long been recognized by fruit growers. Many young fruit trees have been disadvantaged or spoiled by having been planted on the same place as old trees. Through repeated growing of one tree species toxic substances seem to have accumulated in the soil. A rather striking example is provided by peach orchards in California and Ontario, where an explanation has long been sought as to why the yield has gone down after repeated replanting of young trees. Recently, a Canadian research worker. PATRICK (1955), has been able to prove that peach roots secrete into the soil the glycoside amygdalin. which is easily broken down by the soil microbes to glucose, hydrocyanic acid and benzaldehyde. It is a well-known fact that the amygdalin itself could not be harmful to young peach-trees but only its decomposition products and in particular the benzaldehyde.

Another example of soil infertility is provided by German apple orchards. Here also it was easy to suppose that certain toxic substances, secreted from roots, might be responsible among other factors for yield reduction. This assumption is verified by German investigations (FASTABEND 1955, BÖRNER 1958), which showed that the root bark of the apple trees contain a substance, so-called phlorizin, which is leached out by the soil water. This substance and its microbial decomposition products, have been found to have a growth inhibiting effect on young apple trees.

Similar investigations on the soil infertility phenomenon in the citrus orchards in California indicate that the harmful effect on citrus trees may be due, at least partly, to toxic substances secreted or otherwise liberated from the roots.

The soil infertility problem is a rather complicated one which we have here discussed only from the allelopathic point of view. Soil infertility may also be due to plant parasites or the exhaustion of mineral nutrients.

It might be questioned how great a significance the higher plants' effect upon each other has under natural conditions. Physiologically active substances have been demonstrated, isolated and identified. But so far it has not been possible to show that they occur in the soil in an active form. They are secreted from roots into the soil in extremely small quantities, and it is

therefore probable that they are rapidly broken down or inactivated by microorganisms or through the influence of soil colloids. Consequently, the effect of higher plants upon each other directly through root secretions would seem likely, under natural conditions, to be of minor importance. On the other hand it has been assumed, and in some cases also proved, that these secretions may disturb the balance of the microflora in the rhizosphere and, that they may after repeated growth of the same species, alter this balance decisively.

In this connection we may note the results of the experiments in which it has been shown that roots of certain plants secrete a substance which stimulates the hatching of nematode cysts and chemotoxically influences the movements of the nematode larvae. Thus TODD and his co-workers (1949) were able to isolate from living tomato roots physiologically active fractions which strongly stimulated the hatching of the cysts of the potato nematode—the potato and the tomato are both attacked by the potato eelworm, *Heterodera rostochiensis* Wollenw.—and affected the larvae in such a way that they moved towards the tomato roots. Such a strongly active substance was identified by TODD *et al.* as an acid, probably containing a lactone group. The acid, which was named ecleptic acid, was most active in dilutions of $1:10^7$ and $1:10^8$. In addition, TODD *et al.* were also able to isolate from roots of *Solanum nigrum L.* an active substance, which was supposed to be chemically identical with or rather similar to the substance isolated from tomato roots. It had for instance the same effect on the cysts of the potato nematode. A number of synthetic substances were studied but only one, so called anhydrotetronic acid was active in dilution 1:2000. None of these substances, however, had as strong an effect as that of the exudate. Consequently the identity of the active substance cannot be regarded as definitely settled.

It is also to be noted that to some extent the hatching of the potato nematode cysts seems to be brought about by certain grasses.

Further, some Dutch researchers (UHLENBROEK and BIJLOO 1959) have been able to show that populations of certain nematode species, e.g. *Pratylenchus penetrans* (Cobb) Sher. & Allen, are reduced rather strongly in the soil, when *Tagetes* species, and particularly *T. erecta* L., are grown. They also found that an alcoholic extract of *Tagetes* plants had a toxic effect on a number of nematode species: the active substance was found to be α-terthienyl.

When we succeed in producing synthetically the substances now mentioned, we may get reliable means for nematode control. For instance, if the potato nematode cysts can be brought to hatch in the soil and other crops than potato or tomato are grown, the larvae will be doomed to destruction.

From a practical point of view the control by means of "trap crops" of the weed *Striga lutea* Lour. in maize districts provides an interesting example of the importance of root exudates for stimulating dormant seeds of this weed to germinate. In the journal *Crops and Soils* BEYER (1957) reports that *Striga lutea* is a very bad weed in the maize districts of South Africa, India, the Far East and southern and northern Carolina in the United States. The economic losses brought about in South Africa by *Striga lutea* exceed all the losses from maize diseases and pests put together. It is difficult to control *Striga lutea*, partly because of its large seed production, partly because of the long seed dormancy. This, however, can be broken, at least to some extent, by root exudates from certain grasses, soybean and vigna bean (*Vigna*). In South Africa use is made of "trap crops" in order to induce seeds of *Striga lutea* to germinate. The exudates from these crops stimulate the seeds of *Striga* to germinate simultaneously, and the seedlings can then be destroyed by cultivation. The substances exuded from the grass roots are able only to break the dormancy of the seeds, while the substances from roots of soya and vigna beans stimulate germination and then also retard or inhibit the growth of the seedlings.

Experiments at the Department of Plant Husbandry in 1958–1959

In these experiments the effect of root exudates from the following species were studied: couch-grass, winter rape, scentless mayweed, winter rye, and wild oats.

Methods employed

In order to obtain root exudates the plants were grown in washed and sterilized quartz sand in glass funnels. Below the funnels flasks were placed for collecting excess liquid (pure water or nutrient solu-

tions). Funnels and flasks were covered with black paper in order to prevent growth of green algae.

When the experiment started the plants were first watered with a certain quantity of distilled water and then daily with the solution that had run through the quartz sand and been collected in the flasks. Distilled water was added daily, corresponding to the quantity that had evaporated. Half of the funnels were watered exclusively with distilled water, while the other half once a week got a complete nutrient solution. When the experiment was discontinued, the solutions collected in the flasks were sterilized and in some cases concentrated, and then they were tested with regard to their effect upon germination capacity and growth of test plants.

Germination experiments were carried out on filter paper in Petri dishes. Two replications were used, i.e., two per test plant and solution. 20 seeds were placed in every dish. The filter paper was moistened with 8 ml of the solution collected. The experiments were discontinued after 8 days.

In some series of experiments test plants were also grown in quartz sand in pots, which were watered with the exudate solutions. Here the effect upon the growth of the seedlings was studied.

In order to study the effect upon test plants of decomposition products of roots in the soil, the plants were grown during the summer in Mitscherlich pots. Before sowing the soil was fertilized and carefully mixed. During the vegetative period the plants were watered daily with ordinary water and sometimes with a nutrient solution. Surplus solution running through the soil was collected and returned to the pots. During the ripening period the daily watering was reduced. After the harvest the soil was removed from the pots, sifted and put in smaller pots. Soil from pots that had not been planted but otherwise got the same treatment was also put in small pots for control. Test plants were then sown in the pots, so that each species was grown in soil that had been occupied as well as in soil that had not been occupied by plants.

In order further to study the effect upon test plants of the decomposition products of roots, roots were dug out after the harvest, washed and placed in quartz sand in glass funnels. The funnels were kept at room temperature. After some time the roots began to break down. The decomposition products were washed out with distilled water, and the solutions obtained were sterilized and used for experiments with test plants in Petri dishes as previously described.

The material used in these investigations was sterilized as follows:

seeds were steeped for 15–20 minutes in a 0.1 per cent formaldehyde solution and then washed and dried;

other plant material was steeped for 15–20 minutes in an about 1 per cent sodium hypochlorite solution and then washed;

the solutions were heated for a short time to 100°C in a thermostatic oven, then they were kept at room temperature until next day, when they were heated again; usually they were heated three times in succession;

glass material was heated for two hours to 150°C in a thermostatic oven;

quartz sand was washed carefully and then dried at 150°C in an electric oven.

Investigations with couch-grass

The couch-grass is one of our most troublesome weeds. Its great competitive ability seems to depend however not only on its strongly developed vegetative system. Many observations indicate that its rhizomes and roots contain substances with a detrimental effect on other plants. OSVALD (1947) found that on a field where winter rape had been sown, the rape germinated slowly and developed poorly in certain patches where the rhizomes of couch-grass grew rather densely. OSVALD was able to show that extracts from couch-grass rhizomes in very low concentrations had a stimulating effect on germinating rape seeds, somewhat higher concentrations retarded the germination and the development of the seedlings, and in high concentration inhibited the germination altogether. A similar germination and growth retarding effect on clover and lucerne can be observed on field patches containing much couch-grass. KOMMEDAHL *et al.* (1957, 1959), OHMAN and KOMMEDAHL (1960) and LE TOURNEAU and HEGGENESS (1957) have also been able to show that extracts from couch-grass rhizomes have a strongly detrimental effect upon germination and development of certain cultivated plants such as lucerne, wheat, barley, and oats.

Our knowledge of the chemical substances respon-

sible for the toxic effects of the couch-grass is still imperfect. However, GRÜMMER and BEYER (1960) have isolated several phenolic substances from couch-grass rhizomes and roots. Among these p-hydroxybenzoic acid and vanillic acid are the most important. It has been shown that straw of cereals contains similar substances. Mixed into the soil they exhibit a strong toxic effect.

The experiments mentioned above show that the couch-grass contains growth inhibiting substances. The question is, whether rhizomes and roots of couch-grass can secrete into the soil active substances or if it is decomposition products of the "roots" that are able to check germination and growth of other plants. In order to get an answer to this question the following experiment was arranged.

In Petri dishes with winter rape, red clover, spring barley, and charlock the effect on germination and growth of an exudate solution from "couch-grass roots" was tested.

In order to get the exudate, couch-grass rhizomes were collected in the field, washed, sterilized and kept between moist filter papers for some days so as to secure healing of wounds. They were then placed in quartz sand in glass funnels. During a period of 50 days the rhizomes were watered daily, in half of the funnels only with distilled water, in the other half with distilled water and nutrient solution. The exudate collected was then used for germination and growth experiments in Petri dishes. For some of the test plants also an exudate solution concentrated to twice the original concentration was used. The results are given in Table 1.

Table 1. Effect of extract from couch-grass in sterilized quartz sand upon germination and growth of four species.

The exudate washed out with the watering liquid.

Tested plants	Liquid used for watering, without exudate (control); absolute values			Exudate solution; relative values, as per cent of control values		
	Germination, %	Length of roots, mm	Length of shoots, mm	Germination	Length of roots	Length of shoots
	A. Watering liquid (for the funnels) distilled water					
Spring barley	95	77	110	95	139	105
Winter rape	95	51	35	103	201	140
Red clover	80	20	28	66	115	105
Charlock	25	13	25	100	640	150
	B. Watering liquid (for the funnels) nutrient solution					
Spring barley	95	95	131	92	100	86
Winter rape	95	104	65	100	99	88
Red clover	65	24	33	77	86	93
Charlock	47	16	46	79	320	80

As will be seen from the table the germination capacity of red clover and charlock has been considerably decreased, that of rape and barley only slightly or not at all affected by the exudate. The results show a remarkable growth stimulating effect on seedlings by the exudate solution obtained after watering the couch-grass rhizomes exclusively with distilled water. This effect may be explained as follows: some substances may be liberated from dead cells of the cortex, calyptra and root hairs and these substances may have a nutritive effect. Another explanation might be that the exudate solution obtained with distilled water has had such a low concentration that it has had only a stimulating effect. On the other hand the exudate obtained after watering the couch-grass rhizomes with nutrient solution obviously retarded the growth of seedlings of rape, red clover and barley.

The effect of extracts of soils infested with, as well as without, couch-grass was tested upon the germination capacity and on the development of seedlings. Soil samples were collected from a soil characterized as a loam, rich in humus and mixed with sand. The samples of soil with much couch-grass were taken from a poorly cultivated margin of a field, those of soil without couch-grass from an adjacent, well-cultivated part of the same field. The samples were sifted and placed in glass funnels 3000 cm³ of soil in each. The soil was saturated with distilled water and was subsequently watered twice a day with the solution percolating the soil. The leaching was continued for two weeks and then the solutions were concentrated to equal volume. The solutions thus obtained were used for germination experiments in Petri dishes.

As will be seen from Table 2, the solution from soil with couch-grass slightly retards the germination of all the test plants as well as the root growth of red clover and barley and the shoot growth of rape, but possibly stimulates the root growth of rape and charlock and the shoot growth of charlock.

Table 2. Effect of extracts of soils with and without couch-grass upon different test plants.

	Germination substrate watered with solution from soil					
	without couch-grass (control); absolute values			with couch-grass; relative figures as percentage of control		
Tested plants	Germination, %	Length of roots, mm	Length of shoots, mm	Germination	Length of roots	Length of shoots
Spring barley	100	97	91	97	97	101
Winter rape	98	92	25	97	110	91
Red clover	70	35	17	93	96	99
Charlock	75	22	16	87	117	120

The soil extract investigations were completed by growing plants in the two soils with and without couch-grass rhizomes. The soil samples were sifted and carefully mixed with fertilizers and then filled into Mitscherlich pots. Each test plant was grown in both kinds of soils, two pots of each. They were harvested after six weeks, when the vegetative development had begun to slow down.

The results in Table 3 show that the germinaiton is only slightly reduced, but that roots (except of barley) and stems and leaves as expressed in dry weight have increased considerably when grown in soil which has been rich in couch-grass rhizomes. This result might be explained as an effect of an increased content of organic substance in the couch-grass soil as compared with the couch-grass free soil.

Table 3. Development of barley, rape, and charlock in soils which had been respectively free from, and rich in couch-grass.

Tested plants	Germination	Dry weight of roots	Dry weight of shoots
Soil free from couch-grass ıhizomes; absolute values			
Spring barley	100 %	2.40 g	2.98 g
Winter rape	100 %	1.24 g	2.15 g
Charlock	77 %	0.88 g	2.88 g
Soil rich in couch-grass rhizomes; relative figures (percentage of control)			
Spring barley	93	82	105
Winter rape	98	116	110
Charlock	88	117	115

Disregarding the series of experiments in which the test plants were watered with exudate solutions obtained with distilled water, the results now reported may be summarized as follows:

The germination of rape seed was only slightly affected by substances from the couch-grass. The development of the seedlings was somewhat retarded in the exudate solution, while soil extract from soil which had been heavily infested with couch-grass stimulated the growth of the rape plants. Consequently, there seems to be nothing indicating that couch-grass has a detrimental effect on rape, at least not with fertile soils.

In the case of red clover the exudate solution as well as the extract of "couch-grass soil" have reduced the germination capacity and considerably retarded the growth of roots and shoots. The retarding effect of the exudate solution was greater than that of soil extract.

Barley germinated somewhat less well in all the substrates: exudate solution, soil extract and "couch-grass soil" than in the controls. The root development was retarded more than that of the shoots.

Charlock turned out to be the most susceptible of all the tested species. In all the experiments the couch-grass reduced the germination capacity of the charlock seeds. At the same time the root growth of the plants was strongly stimulated and the growth of shoots sometimes stimulated, sometimes retarded. The germination retarding effect of couch-grass on charlock seeds is in good keeping with practical experience at the experimental field of the Department of Plant Husbandry.

Investigations with winter rape and scentless mayweed

With the increased growing of winter rape in Sweden it has become more and more common to find a rich occurrence of scentless mayweed in the winter rape fields and this plant has indeed become the dominant weed in fields of winter rape. It looks as though winter rape and scentless mayweed thrive very well together. This might perhaps be explained by certain cultivation measures. Mayweed-seed, not too old, is light-requiring and autumn-germinating. The great distance between the rows of the rape plants gives the mayweed seeds a much better light environment for

germination than do the rather dense stands of the winter cereals. In addition, the germination and the development of the mayweed seedlings is favoured through the presence of ample quantities of easily available nutrients particularly nitrates. Consequently the heavy application of nitrogen fertilizers to oil crops in the autumn apparently creates good establishment conditions for the mayweed seeds.

However this explanation is hardly sufficient, since it has turned out that no other autumn-germinating weed with a similar germination biology occurs in such a high frequency in the rape fields as does the scentless mayweed. Might it be possible that the mayweed simply is favoured by secretions from the rape roots?

In order to try to get an answer to this question germination experiments with mayweed and winter rape were arranged in Petri dishes on a substrate moistened with solutions of root exudates from winter rape and mayweed. For preparation of the exudate solutions rape and mayweed plants of both species were collected in the field, washed, sterilized and for "wound healing" kept for a few days between moist filter paper. They were then planted in quartz sand in glass funnels. Mayweed was grown for three weeks and rape for four weeks. During this time the exudate solutions were collected in the way previously described. The exudate solutions obtained were then used in germination experiments in comparison with

Table 4. Effect of extract of winter rape (A) and mayweed (B) grown in sterilized quartz sand, upon mayweed and winter rape.

Tested plants	Nutrient solution without exudate; (control); absolute figures			Exudates in nutrient solution; relative figures as percentage of control		
	Germination, %	Length of roots, mm	Length of shoots, mm	Germination	Length of roots	Length of shoots
A. Exudate from winter rape						
Mayweed	92	12	12	89	168	100
Winter rape	92	68	53	104	128	102
B. Exudate from mayweed						
Winter rape	95	54	56	102	139	135
Mayweed	90	20	14	53	103	101

Table 5. Effect on mayweed of soil which had previously carried winter rape or mayweed.

Soil previously planted with	Germination	Length of shoots	Dry weight of shoots
—(control); absolute values	72 %	23 mm	0.8 mg
Winter rape; relative figures	133	123	148
Mayweed; relative figures	83	72	56

nutrient solutions. The results of the germination experiments are given in Table 4.

As will be seen from the figures, the exudate from rape roots had a slightly retarding effect upon the germination of mayweed seeds but strongly stimulated the growth of roots, while the growth of shoots was not affected. The germination and the development of the seedlings of rape were favoured by the rape exudates. The exudate from mayweed had no effect upon the germination of rape seed, but stimulated considerably the development of the rape seedlings. On the contrary, the mayweed exudate strongly retarded the germination of mayweed seeds, while the growth of the seedlings was practically unaffected.

In order to study the effect on mayweed of soils, which previously had carried either winter rape or mayweed, an experiment was arranged with these species in Mitscherlich pots employing the method previously described, i.e., mayweed as a test plant was grown in soils which had previously carried rape or mayweed or nothing. After somewhat more than a month the experiment was discontinued. The results are given in Table 5.

As will be seen from the figures, germination and vegetative development of mayweed are favoured by soil on which winter rape had previously been grown, but strongly disfavoured by soil in which mayweed had been grown.

In order further to study the effect of decomposition products from rape roots upon mayweed, rape roots were leached out with distilled water during the decomposition process in the way previously described. Twice, one week and three weeks after planting, the decomposition products were washed out from the sand. Seeds of mayweed were placed on filter paper in Petri dishes and moistened with the solutions

Table 6. Effect upon mayweed of decomposition products of winter rape washed out from quartz sand with distilled water.

Germination substrate moistened with	Germination	Length of roots	Length of shoots
Distilled water (control)	83 %	4 mm	9 mm
Extract solution, relative figures, percentage of control	92	301	134

obtained and with distilled water. Since both of the solutions had about the same effect only the mean values from the two series are given in Table 6.

The figures show that the solution obtained slightly retarded the germination but strongly stimulated the growth of the seedlings. The stimulation might partly be explained as a nutritive effect.

The experimental results now briefly reported might be summarized as follows: the exudate solution from rape roots and the decomposition products left behind in the soil or washed out in solution, contain physiologically active substances as well as some plant nutrients. These substances have a favourable influence on the development of mayweed seedlings. It seems probable that these substances are not actively secreted from the roots but are liberated from dead cells of cortex, calyptra and root hairs. The effect of these substances in the field may be confined to the immediate surroundings of the roots.

It should be mentioned here that MARTIN and RADEMACHER (1960) have found that root remains of rape favour the growth of wheat roots. They were also able to show that the mustard oil glycoside, which is regularly present in the rape seeds also occurs in the roots. Mixed into the soil in small quantities it stimulated the growth of wheat.

Investigations with winter rye and wild oats

On soils where wild oats nowadays is common, it can easily be observed that this plant rarely occurs in winter cereals, particularly not in fields with winter rye. This is in good agreement with agricultural experience (cf. above). The retarding effect of winter cereals and particularly rye, upon wild oats might partly be explained as the result of competition for nutrients, water and light. The wild oats germinate in the spring, when the autumn-sown cereals have already got far in development and apparently have strong competitive ability in relation to the wild oats seedlings. The superiority of the winter rye and its ability "to kill the wild oats" has been explained by its rapid growth and its capacity to form dense stands. This however cannot be the whole explanation, and many observations seem to indicate that the effect is due to secretions from the rye roots.

Good support for this conception was given by a rather simple experiment. In the spring of 1959 the following plots were sown with marker on a well fertilized soil in the experimental field: (1) winter rye (King II) and wild oats (from Östergötland) separately in pure stands and (2) winter rye and wild oats together The distance between the rows was 11 cm and between the plants in the row 5 cm. Of both species two grains were sown in each marked hole. The germination was about the same for both species, varying between 90 and 100 per cent. The rye germinated somewhat more quickly than the wild oats but only formed rosette shoots. Straws did not develop, so that there was no overshadowing from the rye plants.

In the beginning the wild oats plants developed normally on the plot with the mixed stand, but soon growth came to a stillstand and an obvious retardation could be observed. Seven weeks after sowing the experiment was harvested. The following results were obtained:

	Dry weight of plants g	relative figures
Rye in pure stand	0.55	100
Wild oats in pure stand	0.42	100
Rye in mixed stand	0.50	90
Wild oats in mixed stand	0.18	43

In subsequent laboratory experiments the effect of rye exudate solution upon germination and development of seedlings of wild oats was studied. Winter rye was grown in glass funnels with quartz sand and watered with (1) distilled water only, and (2) distilled water and nutrient solution. The run-off solution from the funnels was then used in germination experiments in Petri dishes. The results are given in Table 7: I.

As will be seen from the figures the rye exudate collected in distilled water has favoured germination

Table 7. Effect of extract from rye grown in sterilized quartz sand upon germination and development of wild oats.

The exudate washed out with the watering solution.

	Germination	Length of roots	Weight of roots	Length of shoots	Weight of shoots
A. Watering liquid distilled water					
I. Germination substrate moistened with					
Watering liquid (control)	85 %	18 mm	1 mg	100 mm	4 mg
Exudate solution, relative % figures	112	262	120	107	100
B. Watering liquid nutrient solution					
Watering liquid (control)	95 %	84 mm	2 mg	126 mm	5 mg
Exudate solution, relative % figures	92	78	76	92	90
II. The quartz sand moistened with					
Nutrient solution without exudate (control)	100 %	216 mm	18 mg	260 mm	14 mg
Exudate in nutrient solution, relative % figures	92	75	53	92	74

and growth of wild oats, as compared with the control with distilled water, but the rye exudate in nutrient solution has obviously retarded both germination and growth of wild oats. The results of the first series may be explained as a nutritive effect as in previous experiments of the same type. In the other series, where the differences in nutrition have been smoothed out, the retarding effect of the exudate is rather pronounced.

In another experiment the rye exudate in nutrient solution was used for watering wild oats grown in pots with quartz sand. Plants for control were watered with the nutrient solution. In each pot, two for each treatment. 20 grains of wild oats were placed. The experiment was run for a month and then harvested. The results are given in Table 7: II. It is evident that also in this experiment the rye exudate has had a considerable retarding effect upon germination and particularly upon the growth of wild oats.

The development of wild oats seedlings was also studied in soils which had carried rye or no crop at all. In this experiment the method previously described for experiments of this kind was employed. In each pot, two for each treatment, 20 grains of wild oats were planted. The experiment was run for a month and then the length and dry weight of the wild oats shoots was measured. The result was:

	Length of shoots	Dry weight of shoots
From soil without a crop	247 mm	13 mg
From soil in which winter rye had been grown, relative % figures	75	56

If compared with the results of the preceding experiment it is obvious that rye roots may leave behind substances having a retarding effect on the growth of wild oats.

In order further to study the detrimental effect on wild oats of decomposition products from rye roots a germination experiment in Petri dishes was carried out. The germination substrate was moistened with a solution washed out from decomposing rye roots. The solution was obtained in the way previously described and the decomposition lasted for six weeks. The results are given in Table 8.

Since in this experiment distilled water was used, the retarding effect of the extract is obscured, by growth promoting (nutrient) substances in the solution. In addition, it is a well known fact that wild oats germinates better in a nutrient solution than in distilled water, a fact that also seems to have an effect in this case.

The experimental results now briefly reported indicate that rye roots contain one or more substances with a retarding effect upon germination and particularly on the growth of wild oats. These substances may be secreted from living roots or be washed out

Table 8. Effect upon wild oats of decomposition products from winter rye roots, washed out from quartz sand with distilled water.

Germination substrate moistened with	Germination	Length of roots	Weight of roots	Length of shoots	Weight of shoots
Distilled water (control) absolute values	85 %	128 mm	2 mg	101 mm	4 mg
Extract, relative % figures	108	92	90	97	97

from dead roots and are left behind in soil which has carried winter rye. Whether they are actively secreted from living roots or passively liberated from roots can hardly be settled. None the less the results now presented are in good conformity with the practical experience that rye retards the growth of wild oats.

Discussion

With the methods employed in the experiments, the results of which have now been presented, it is not possible to decide whether the physiologically active substances are real secretions from living cells, exudates, or whether they are passively liberated from dead cells of cortex, calyptra or root hairs. They might well be both. Since the substances emitted from living roots essentially seem to have the same effect as extracts from dead roots, it is reasonable to suppose that the substances are predominantly liberated from dead cells or have in some other passive way reached the substrate or the solution. But if the roots really exude certain substances, it is also reasonable to suppose that these may be liberated unchanged from dead cells together with certain other substances which are not being exuded.

To settle the question whether the active substances are real exudates or passively liberated from decomposing dead cells, another method than that we have used must be employed, for instance the method followed by EBERHARDT and MARTIN (1957), i.e., to study living roots by a fluorescence microscope. From a plant ecological viewpoint, however, it is of no significance whether the physiologically active substances are really secreted or if they are passively liberated.

It is of course of great interest to find out what these substances are that exert a physiological effect upon other species. In connection with the experiments here reported the substances have been studied by means of paper chromatography, although so far no definite results have been obtained. We have been able to identify amino acids and sugars etc., but not yet any other specific substances.

The experiments concerning the effect of couch-grass upon a number of cultivated plants seem to indicate that in this case several factors interact in a rather complicated way. Since the substances obtained from living roots of couch-grass have had a relatively small retarding effect—at least in the concentrations we have used—it seems to be most likely that the yield reducing effect of couch-grass is due in the first place to its ability successfully to compete with the cultivated plants for space, light and nutrients. But if so, it is nevertheless conceivable that the detrimental effect of the substances from the couch-grass roots is likely to reinforce the competitive ability of the couch-grass by giving it an advantage which it otherwise might not have. From this point of view it might be of interest to study the influence of couch-grass not only upon the germination and seedling development of cultivated plants but also upon the penetrative ability of the shoots. In fact certain circumstances seem to indicate that the detrimental effect of the physiologically active substances is greater in the field than under the rather favourable conditions for germination and growth offered in the laboratory experiments. This is particularly clear in the comparison between the laboratory experiments and the field experiment with wild oats.

In this connection it should be emphasized that the lack of agreement between field observations and results of laboratory tests may be due to differences in the concentration of the exudates. As previously shown, in low concentration the couch-grass extract has a stimulating, but in strong concentration a retarding effect. On this account definite conclusions cannot be drawn from the laboratory experiments until it has become possible to establish the concentration of the exudate solution; for this purpose the active substance must first be identified.

Further, it should be considered, that it might be possible that the heating of the exudate solutions to 100°C may have some influence on the active chemical substance. Consequently it is proposed in subsequent research also to try other methods for sterilization, for instance filtering through bacterium filters.

However, it seems to be most important, when the active substance has been identified, to work with different concentrations of this substance and if possible to compare these with the concentrations occurring in the soil.

Between rape and scentless mayweed interesting relationships prevail. Both of the species favour each other, but mayweed plants are slightly disfavoured by exudates from itself, which is not the case with rape plants. The abundant occurrence of mayweed in rape fields may therefore be explained as due to the

fact that the rape neutralizes the retarding effect of the mayweed plants upon each other. Owing to the favourable effect of mayweed upon rape this crop plant developes well and yields fairly well even though mayweed may occur abundantly and provide considerable competition for space, light and nutrients.

With regard to the stability of the active substances in the soil so far very little is known. Only very few substances with toxic effect have been isolated from soils. It is rather likely that many of the physiologically active substances are broken down comparatively easily by the microflora or are adsorbed by the colloids of the soil. The effect in the soil of the active substances may, therefore, at least in many cases, be restricted to the close neighbourhood of the roots. On the other hand it is obvious that some substances causing soil infertility remain stable for a long time in the soil.

Summary

In the years 1958 and 1959 the effect of root exudates and decomposition products of roots of couch-grass, winter rape, scentless mayweed, wild oats and winter rye were investigated at the Department of Plant Husbandry of the Royal School of Agriculture. The five species were grown (*a*) on quartz sand, from which the solution running off after watering was collected, and (*b*) in soils treated in different ways. Decomposition products were washed out from roots which had been lying for some time in quartz sand at room temperature. The effect of the substances obtained was studied on test plants in Petri dishes (germination experiments) and in Mitscherlich pots.

The following results were obtained:

1. The substances obtained from rhizomes and roots of couch-grass had the following effects:
   (*a*) *on rape*. The seed germination was only slightly affected, but the development of the seedlings was somewhat retarded by the exudate solution while soil extract and soil which had previously carried much couch-grass, seemed to favour the growth.
   (*b*) *on red clover*. The different solutions as well as soil, which had previously carried much couch-grass had an obviously retarding effect upon germination and seedling growth.
   (*c*) *on spring barley*. The germination was only slightly retarded by the different substrates. The root development of the seedlings was somewhat retarded, while the shoot development was not affected or was somewhat favoured.
   (*d*) *on charlock*. The germination was considerably reduced by all the substrates, the root growth was strongly stimulated, and the shoot development was retarded.
2. Exudates and decomposition products of rape roots
   (*a*) somewhat reduced the germination of scentless mayweed seeds but strongly favoured the growth of the seedlings,
   (*b*) stimulated the development of the rape seedlings.
3. Exudates and decomposition products of scentless mayweed roots
   (*a*) favoured the development of rape plants,
   (*b*) reduced the germination of mayweed seeds and retarded the growth of the seedlings.
4. Exudates and decomposition products of rye roots reduced the germination of wild oats grains and strongly retarded the development of young plants.

Many of the results obtained are in good coincidence with observations and experience from farming practice. Some of the results seem to indicate that the exudate solutions in very low concentrations are growth stimulating, while in higher concentrations they are growth retarding.

It is difficult to decide to what extent the physiologically active substances exuded from the roots are specific secretions or substances liberated from dead cells of cortex, calyptra or root hairs.

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Corrections

Page 7, column 2, line 18. *Change* "1940" *to* "1958".

Page 18, column 1. *After* "BEYER, E., Corns ... 1957" *add* "BODE, H. R., Über die Blattausscheidungen des Wermuts und ihre Wirkung auf andere Pflanzen. — Planta, 30. 1940".

Page 18, column 1, line 5. *Change* "1940" *to* "1958".